

A BIOMETRIC RE-EVALUATION OF THE SILURIAN BRACHIOPOD LINEAGE *STRICKLANDIA LENS/S. LAEVIS*

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ABSTRACT. Quantitative data from Norway, Estonia, and the Llandovery area in Wales are used to re-evaluate the existence of the *Stricklandia lens*/*S. laevis* part of the *Stricklandia*/*Costistricklandia* evolving lineage. Two of the directed trends originally used to discriminate subspecies in material of the type Llandovery area fall within the same range of variation at roughly contemporaneous horizons in the Lower Silurian of Norway, Wales, and Estonia. These are reduction of the outer plates relative to the inner plates, and reorientation of the inner plates. A third trend in the Llandovery material, increasing size of cardinalia, does not occur in the Norwegian material and is regarded as environmentally determined. The stricklandiids show large phenotypic variation within sample populations and correlation must be based on a minimum of ten specimens. The four lowermost subspecies of Williams (1951) occur abundantly in a nearly continuous section in Norway, providing material for refined biocorrelation through an index combining the two evolutionarily valid trends.

GOULD AND ELDREDGE (1977) listed the essential criteria for an adequate test of evolutionary models: good geographic coverage, long sequences of closely spaced samples, unambiguous definition of taxa, and adequate biometrical testing on a sufficiently large database. Few if any studies on macrofossils were found by Gould and Eldredge to meet all these requirements. Arnold (1966) and Johnson and Colville (1981) further stressed the importance of tests for simultaneous occurrence in different geographical localities in order to exclude the presence of non-evolving geographical clines. In addition, Sadler (1981) and Schindel (1982) showed that sedimentary sequences with frequent periods of non-deposition and erosion are more the rule than the exception, thus making the validity of most micro-evolutionary studies questionable. Even if the micro-evolutionary patterns involved cannot be fully revealed, however, evidence for the widespread existence of a lineage is valuable as a tool for biostratigraphic correlation. The existence of a lineage must be tested following the criteria mentioned above, although a lower degree of resolution may be sufficient for practical applications in chronostratigraphy. The purpose of this contribution is to test the validity of parts of the often cited *Stricklandia*/*Costistricklandia* lineage in the Lower Silurian of Norway, Estonia, and Wales.

PREVIOUS WORK

Kiær (1908, pp. 499–501) was the first to suggest a stricklandiid lineage based on material in Norway. This was later expanded and confirmed in the classic work of Williams (1951) on the Llandovery area of Wales. Rubel (1977) found and described the same lineage from Estonia while Johnson (1979) found parts of the lineage in Iowa. Representatives of the *Stricklandia*–*Costistricklandia* lineage have a widespread distribution in the Lower Silurian occurring in North America (Berry and Boucot 1970), the British Isles (Ziegler *et al.* 1974), eastern Europe, especially the Baltic region (Kaljo 1979), and Scandinavia (St. Joseph 1938; Bassett and Cocks 1974). Although the taxa are widespread, well described, and the lineage is widely employed, a detailed biometric study has never been attempted.

All earlier studies on the *Stricklandia*–*Costistricklandia* lineage have shown that the features of evolutionary significance occur in the internal structures of the cardinalia while external features show great plasticity. Shell shape or length of the interarea are therefore of little systematic value (Kiær 1908; St. Joseph 1935; Williams 1951; Johnson 1979).

The lineage includes five stricklandiid taxa based on features in the cardinalia, from the oldest *S. lens prima* Williams, 1951 through *S. l. lens* (J. de C. Sowerby, 1839), *S. l. intermedia* Williams, 1951, and *S. l. progressa* Williams, 1951 to the youngest *S. l. ultima* Williams, 1951. The latter was considered by Cocks (1978) to belong to a separate species, *S. laevis* (J. de C. Sowerby, 1839), with a transitional position to *C. lirata* (J. de C. Sowerby, 1839).

The taxa of the lineage treated by Williams (1951, p. 88) represent according to him 'simply four stages of development that the species passes through during its existence' and 'the choice of these particular stages has been dictated by convenience and not by more objective considerations'.

OCCURRENCE OF STRICKLANDIIDS

All representatives of the *Stricklandia*-*Costistricklandia* lineage are present in the Llandoverly succession of the Oslo Region in Norway. The Asker District, lying south-west of Oslo (text-fig. 1A, B), is the main area for this study because all taxa are well represented there. They also occur in the Oslo, Ringerike, Holmestrand, and Skien districts (text-fig. 1A).

The Llandoverly of the central Oslo Region consists of the oldest Solvik, middle Rytteråker, and youngest Vik formations. In the Asker District stricklandiids occur very rarely from 11 m to 95 m above the base of the Solvik Formation but from this level to the top of the formation they are very abundant. At Sandvika, 5 km north of the main investigated area (text-fig. 1B), abundant stricklandiids occur where the Solvik Formation is exposed, except in the basal beds. They occur both in mudstone and in limestone intercalations. In limestone they are often articulated and in their growth position. In mudstone they are mostly disarticulated but there are few signs of distant transport.

Stricklandiids are only common in the overlying Rytteråker Formation in a 1.5 m thick shale interbed in the middle of the otherwise calcareous formation in the Skien District. The specimens occur in a transported and mixed benthic assemblage. The same kind of occurrence within shaly interbeds can be seen at the base of the Vik Formation at Sandvika and at Malmöya in the Oslo District.

The Vik Formation of Asker, Skien, and Ringerike yields *Costistricklandia* which is also found at the top of the overlying Bruflat Formation at Ringerike. The specimens occur in nests *in situ* in calcareous interbeds.

BIOSTRATIGRAPHIC FRAMEWORK OF THE NORWEGIAN SECTIONS

Table 1 shows the main fossil taxa used for biocorrelation in the Llandoverly of the Asker area, the data taken mainly from Worsley *et al.* (1983). These data suggest that the base of the Solvik Formation in the Asker District lies close to the base of the Silurian. This is supported by a basal fauna with a strong Ordovician aspect mixed with a few typical Silurian species (Baarli and Harper, in press). Beds occurring 170 m above the formational base are certainly younger than the uppermost *atavus* biozone, and probably as young as the *cyphus* biozone. A level 211 m above the base could still be within the *cyphus* biozone, but is probably of *gregarius* biozone age since conodonts and brachiopods in the topmost 20 m of the 245 m thick formation are indicative of, or close to, the *sedgwickii* graptolite biozone. The occurrence of stricklandiids at the base of the Vik Formation must lie between mid-*sedgwickii* to basal *turriculatus* graptolite biozones.

SEDIMENTARY SETTING OF THE SOLVIK FORMATION IN THE ASKER DISTRICT

The lithostratigraphy and sedimentology of the Solvik Formation are described in detail by Baarli (1985). The lower 170 m are fairly uniform and consist of medium to thickly bedded mudstone with very thin to thin calcareous siltstone to silty limestone interbeds (the Myren Member) and more pure limestone interbeds (the Spirodden Member). The upper 75 m thick Leangen Member starts with a 20 m thick, very shaly sequence which grades into medium to thickly bedded mudshale with thin to medium thick storm-derived silt to fine sandstone intercalations (all references to thickness of beds follow the scheme of Ingram 1954). There are no clear indications of major pauses in sedimentation or erosional gaps, but the most likely horizon is the transition between the lower 170 m and the upper 75 m. Here the change in lithology is very abrupt.

Sedimentological studies and palaeoecological analysis suggest a storm-dominated platform with two main shallowing up sequences separated by a deepening; another less pronounced deepening occurs at the top of the formation (Baarli 1985). The topmost shallowing-up sequence was deposited in a shallower and more proximal

TABLE 1. The biostratigraphically important taxa in the Llandovery of the Oslo and Asker districts. Where occurrences are referred to the stages of Cocks *et al.* (1970) in the literature these are correlated to graptolite biozones by the author.

GRAPTOLITES	CONODONTS	BRACHIOPODS
201–211 m Solvik Fm. <i>Coronograptus</i> cf. <i>cyphus</i> , <i>Lagarograptus acinaces</i> ? <i>Pribylograptus</i> ex gr. <i>sandersoni-incommodus</i> . The assemblage suggests a <i>cyphus</i> or <i>gregarius</i> biozone (Worsley <i>et al.</i> 1983)	Middle of Vik Fm. <i>Pterospathodus pennatus</i> <i>pennatus</i> , <i>P. amorphognathoides</i> . The two mark the transition between the <i>celloni</i> and <i>amorphognathoides</i> conodont biozones which occurs in the <i>crenulata</i> graptolite biozone of Great Britain (Aldridge and Mohamed 1982)	23–43 m Vik Fm. <i>Pentamerus</i> to <i>Pentameroides</i> . The evolutionary transition from <i>Pentamerus</i> to <i>Pentameroides</i> is dated to the <i>griestoniensis</i> graptolite biozone in Great Britain (Ziegler <i>et al.</i> 1974)
170–211 m Solvik Fm. <i>Rhaphidograptus toernquisti</i> . Occurs in <i>atavus</i> to <i>sedgwickii</i> biozones (Rickards 1976)	243 m Solvik Fm. <i>Distomodus</i> aff. <i>D. stauognathoides</i> . Similar specimens are seen in the <i>sedgwickii</i> graptolite biozone of Great Britain (Aldridge and Mohamed 1982)	64 m Rytteråker Fm. <i>Pentamerus</i> . Evolution of cardinalia suggests a middle <i>sedgwickii</i> graptolite biozone. (Baarli and Johnson 1982)
170 m Solvik Fm. <i>Orthograptus obuti</i> . Found in the Urals of probable <i>cyphus</i> biozone age (Rickards and Koren 1974)	235 m Solvik Fm. ' <i>Amorphognathus</i> ' <i>temuis</i> . Common in the <i>argentus</i> to mid- <i>sedgwickii</i> graptolite biozones in the Llandovery type area (Aldridge and Mohamed 1982)	From 236 m Solvik Fm. <i>Gotatrypa hedei</i> . Makes its first appearance in topmost <i>convolutus</i> graptolite biozone (Copper 1982)
11 m Solvik Fm. <i>Climacograptus transgrediens</i> Suggests latest <i>persculptus</i> to earliest <i>acuminatus</i> biozones (Howe 1982)	8–243 m Solvik Fm. <i>Ozarkodina oldhamensis</i> . Has been proposed to define the base of the Silurian on Anticosti Island (Barnes 1982)	220 m Solvik Fm. <i>Eopholidostrophia cocksi cocksi</i> . Evolves into <i>E. c. ultima</i> at the top of the <i>convolutus</i> graptolite biozone in Great Britain (Hurst 1974)

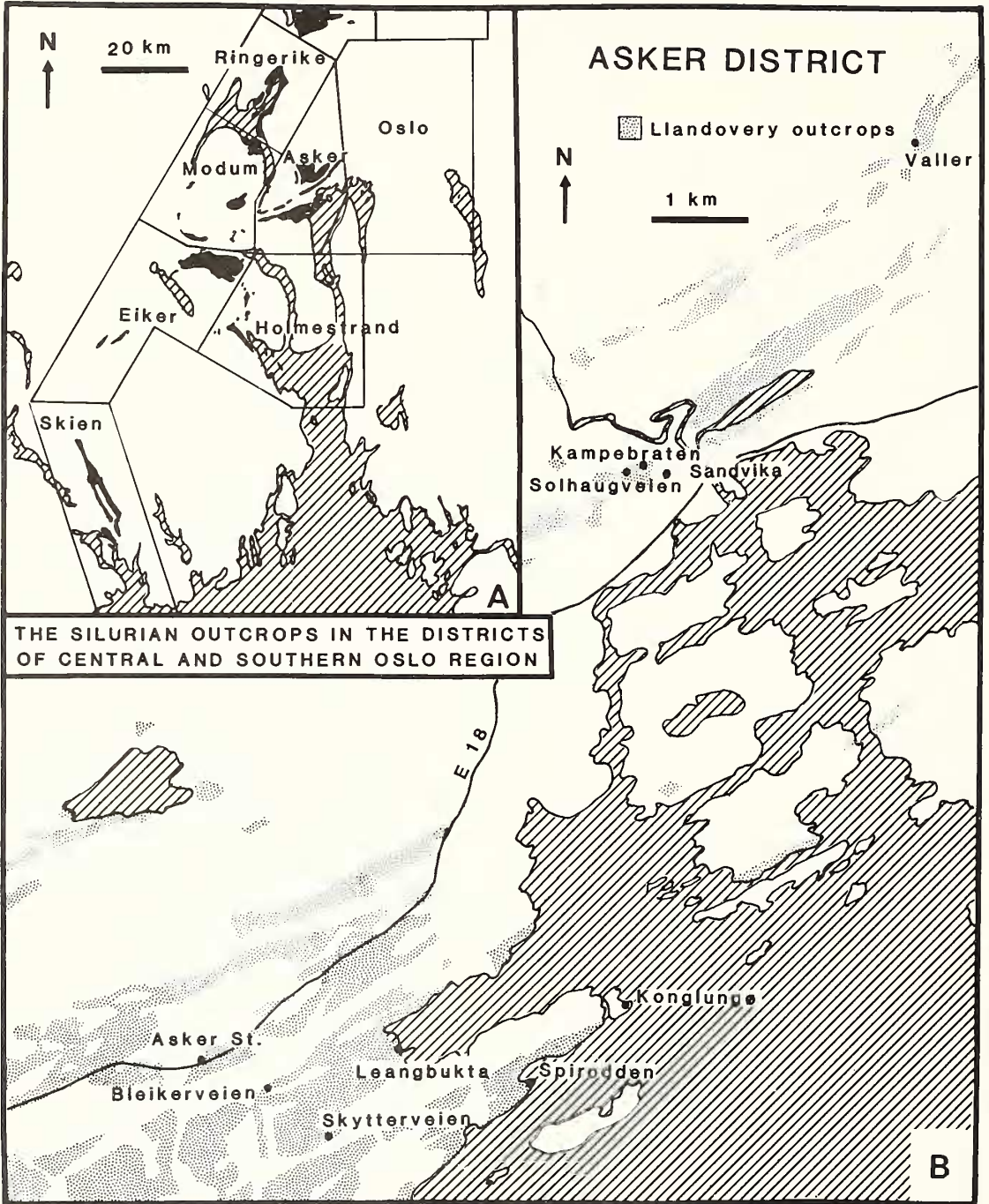
environment than the lower sequence. The sections are physically correlated by frequency of storm-derived silt and fine sandstone interbeds which are regarded as locally synchronous.

MATERIAL AND METHODS

The Solvik Formation in the area east of Asker Station was sampled at Spirodden (grid. ref. NM826339), Skytterveien (NM820339), and Leangbukta (NM826342) (text-fig. 1B). The three sequences are located within 2 km of each other and constitute a composite section through the upper 235 m of the complete 245 m thick Solvik Formation. The material was retrieved mainly from 5 to 10 kg bulk samples collected at 2.5–5.0 m intervals throughout the upper 150 m of the Solvik Formation where stricklandiids are abundant. Each bulk sample was collected in mudstone or mudshale with a maximum thickness of 20 cm. Additional spot sampling over a 5 m interval was done where stricklandiids appeared to be sparse. One large sample for population studies was taken on a bedding plane.

In Sandvika spot sampling was done in a 80 m thick section through the upper part of the Myren Member and the lowermost 70 m of the Spirodden Member of the Solvik Formation. Bulk samples of approximately 5 kg were collected in the top 25 m of the formation. A 20 kg bulk sample was collected in the basal Vik Formation at Kampebråten (NM848403) and spot sampling was done at the same level at Vallerkroken (NM858423).

The type material described by Williams (1951) from the Llandovery type area and the Estonian material described by Rubel (1977) were also treated for comparison.



TEXT-FIG. 1. A, districts and Silurian outcrops in the central and southern Oslo Region, Norway. B, sampling sites and Llandoverly outcrops in the Asker District.

The Norwegian material was disaggregated into small pieces and all shell material dissolved in 8% HCl. Thereafter the stricklandiid material was soaked in a piolodofom bath in a pressure tank for 24 hours and dried at 110 °C for 4 hours to induce hardening. Latex casts were made from the brachial valve moulds of both the Norwegian and the already prepared Llandovery material. The whole procedure involved a 20–60% loss of material where the delicate structures in the cardinalia were destroyed. The Estonian material consisted of shell fragments washed out from core sediment. Eight different measurements were made on the casts (in the case of the Estonian material directly on the shells) using an eyepiece scale in the microscope at 16× magnification. The measurements were made without knowledge of the stratigraphic horizon whenever possible for the Norwegian material and always for the Estonian and the Llandovery material. The measurements include:

- a*, the length from the posterior point of the cardinalia to the anterior point of the outer plates.
- b*, the length from the posterior point of the cardinalia to anterior point of the inner plates, where they are fused with the brachial processes.
- c*, the height measured from the anterior point of the inner plates where they are fused with the brachial process vertically down to the base of the valve floor.
- d*, the distance between the anterior points of the outer plates.
- e*, the distance between the anterolateral points where the inner plates are fused with the hingeline.
- f*, the distance from the posterior point of the cardinalia to the anterior point of the inner plate on the lateral side, where it is fused with the hingeline.
- g*, the maximum length of the interarea.
- h*, the maximum width of the brachial valve.

Where possible all these measurements were made, but the external measurements (*g* and *h*) were often difficult, and were impossible in the Estonian material. The populations were often small and form indexes are used to avoid very scattered results caused by random differences in size between small populations. To standardize, all the other measurements on the cardinalia are compared with *b*, a variable which by trial seemed to undergo little change through time. This gave five form indexes: a/b , c/b , d/b , e/b , and f/b . In addition the indexes e/g and e/h were also studied. A combination index $(a + c)/b$ turned out to be most useful for purposes of practical correlation. Since external measurements are scarce, a gross check on general differences in size through time was accomplished by clustering all specimens of each subspecies for comparison with each other.

In total, measurable latex casts were made from 391 specimens in 32 samples collected within the upper 150 m of the Solvik Formation in the main Asker area. Sample size varied from 1 to 67 individuals. In addition, 79 individuals from 9 samples from the middle and upper members of the Solvik Formation, and 12 individuals from 2 samples at the base of the Vik Formation were retrieved and measured from the Sandvika area in the Asker District. All the Norwegian material is stored at the Palaeontological Museum in Oslo. The numerical data are deposited with the British Library, Boston Spa, Wetherby, Yorkshire LS23 7BQ, UK as Supplementary Publication no. SUP 14027 (63 pages).

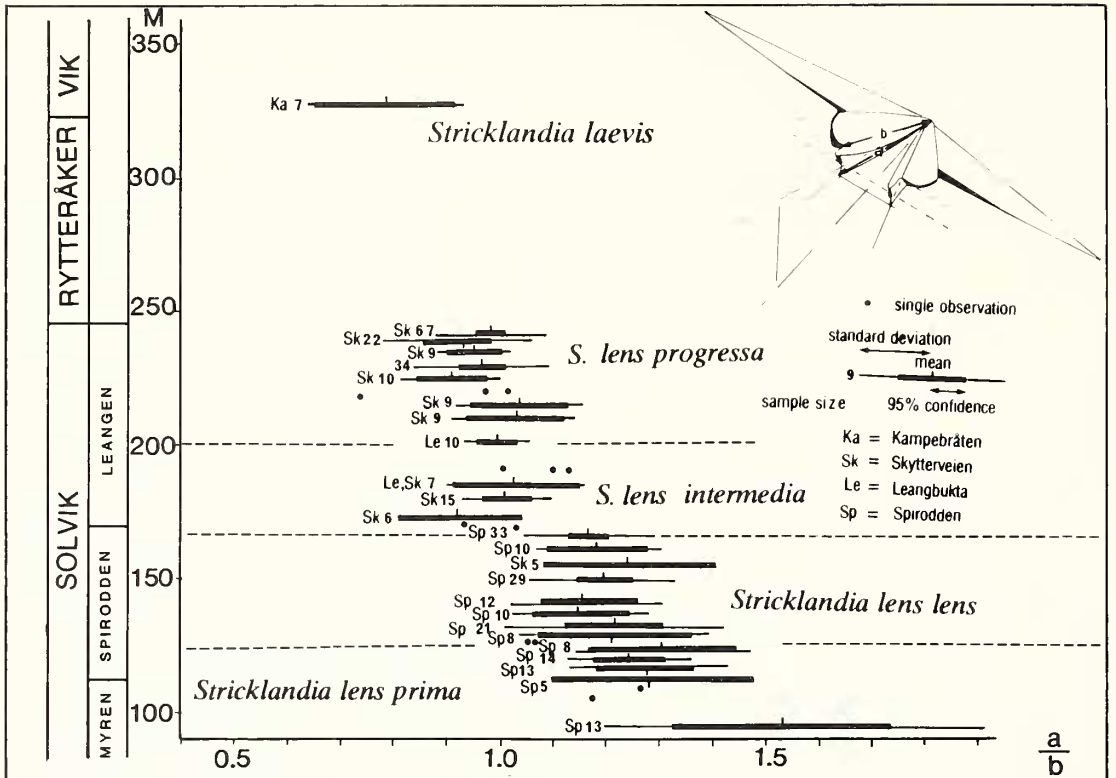
Samples of less than five individuals were not treated statistically in the main Asker area, but were included in the Sandvika area since material there was much scarcer. Sample mean, standard deviation, and the 95% confident interval were calculated for each sample and form index, and then plotted against stratigraphic level. Simple tests, such as t-test for significant differences between the lowermost and uppermost sample, and the Spearman rank test for trends, were applied to establish the statistical significance of morphological trends.

Since much phenotypic variation is represented in the material the mean of the index $(a + c)/b$ is plotted against number of specimens counted in four of the largest samples to test for adequate sample size (text-fig. 9).

The largest sample, at 241 m above the base of the Solvik Formation in the main Asker area, provided material for an analysis of how the form indexes are dependent on size of the specimens. This sample was collected from a single bedding plane and is thus closest to a natural population. The different form indexes were plotted against maximum width and against length of the interarea. T-tests and correlation coefficients were calculated (Table 2). If maximum width or length of interarea are taken as a measure of age, then heterochrony can be detected.

Only seventeen specimens of the Llandovery type material were treated. These include about half of the types of the dorsal valves listed by Williams (1951). The rest were either not available or satisfactory latex casts could not be obtained. Unfortunately none of the types of *S. lens prima* were available. Form indexes were calculated and grouped relative to the subspecies erected by Williams (1951).

The Estonian material embraces 105 individuals from boreholes in nine different geographical localities. The material was treated in the same way as the Norwegian material. Each borehole contained from two to four subspecies. Since the boreholes can not be adequately correlated and each borehole contains few specimens, the material was grouped in successive subspecies as determined by Rubel (1977).

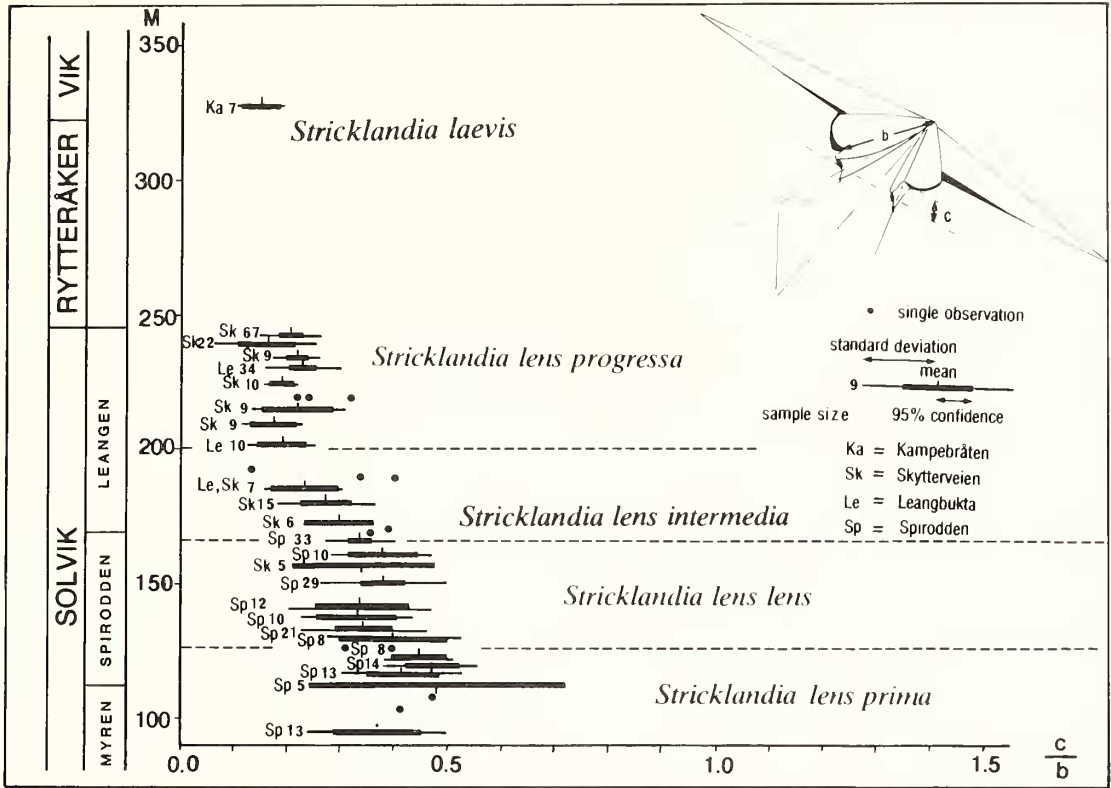


TEXT-FIG. 2. Mean, standard deviation, and 95% confidence intervals of form index a/b for all stricklandiid samples with sample size 5 or more in the Solvik Formation of the main Asker area, plotted against stratigraphic level. For comparison one sample from the Vik Formation in Sandvika is included.

BIOMETRIC ANALYSES

The main Asker area

Text-figs. 2-7 show the statistically treated form indexes for material from the main Asker area plotted against stratigraphic level. T-tests between the lowermost sample at 95 m and the uppermost sample at 241 m show that there is a highly significant difference in morphology between the two samples ($P < 0.001$) for the form indexes a/b and c/b (text-figs. 2 and 3). This is accompanied by a clear indication of a decreasing trend found using the Spearman rank test ($P = -91$ for both samples). The t-tests also show a significant difference between lowermost and uppermost sample for d/b and e/g ($P = 0.01-0.001$ and $P = 0.02-0.05$, (text-figs. 4 and 5) respectively). Tests by Spearman rank indicates only a suggestion of a trend for d/b ($P = -41$) and no directed trend for e/g ($P = +0.16$). All the other form indexes (e/b , f/b , and e/h) show no significant differences between the lowermost and uppermost sample and no indication of a directed trend (at least not if the whole sequence is considered). They are therefore regarded as varying about a constant. The two clearest decreasing indexes are combined in the index $(a+c)/b$ which shows a stronger and more even trend than for either of the two singly. The Spearman rank is very high ($P = -96$) and the difference between the lowest and highest samples is at a significance level of $P < 0.001$. To help show how the trends observed for the older parts of the main Asker section seem to continue through younger strata, a sample from the base of the Vik Formation in Sandvika, 5 km to the north, is included in text-figs. 2-7. The trends are clearly observed for a/b , c/b , $(a+c)/b$, and also d/b .



TEXT-FIG. 3. Mean, standard deviation, and 95% confidence intervals of form index c/b for all stricklandiid samples with sample size 5 or more in the Solvik Formation of the main Asker area, plotted against stratigraphic level. For comparison one sample from the Vik Formation in Sandvika is included.

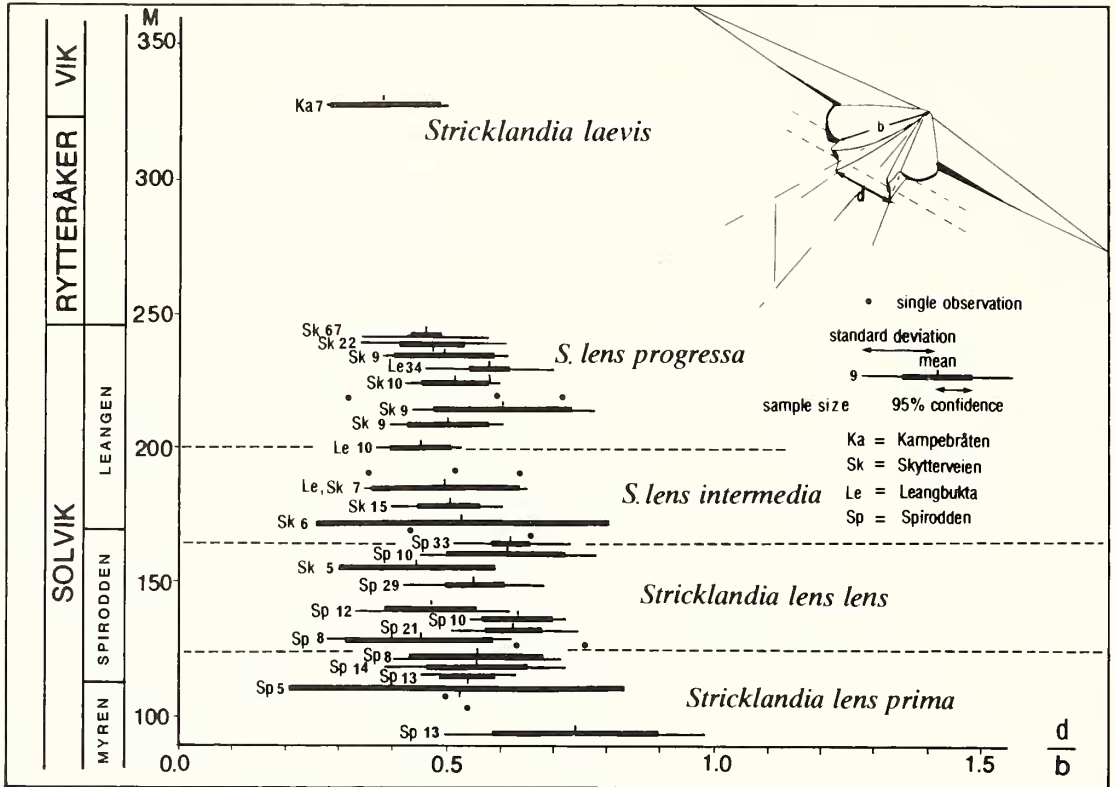
Text-figs. 7 and 8 show that there is a very large phenotypic variation within the samples for form index $(a + c)/b$. This means that the phenotypes on the periphery of different subspecies overlap and occur at the same stratigraphic levels. Text-fig. 8 shows that the mean stabilizes at 15 to 20 measured specimens and this would be a safe sample size to define the average phenotype. So large a sample, however, is difficult to obtain and further inspection of the curves indicates a minimum requirement of ten specimens to ensure an approximately correct form index.

An analysis of size dependence on the form indexes on one sample (Sk241) from a single bedding plane, gave a clear correlation in only one case (Table 2). Maximum width was positively correlated with the form index c/b (correlation coefficient of 0.5749 and a probability of near 0.001). Average maximum width shows no clear trend through the formation (text-fig. 9). The steady decrease in c/b found up through the section therefore cannot be caused by a gradual change in maximum valve width.

The Sandvika area

In the Sandvika area of the Asker District, measurable stricklandiids are found at three different levels in the succession. There are again clear decreasing trends in a/b , c/b , $(a + c)/b$ (text-fig. 10), and d/b .

Comparison of the form index $(a + c)/b$ between the main Asker area and the Sandvika area shows that the index from the lowest level (40 to 70 m above the base of the middle Spirodden Member) is



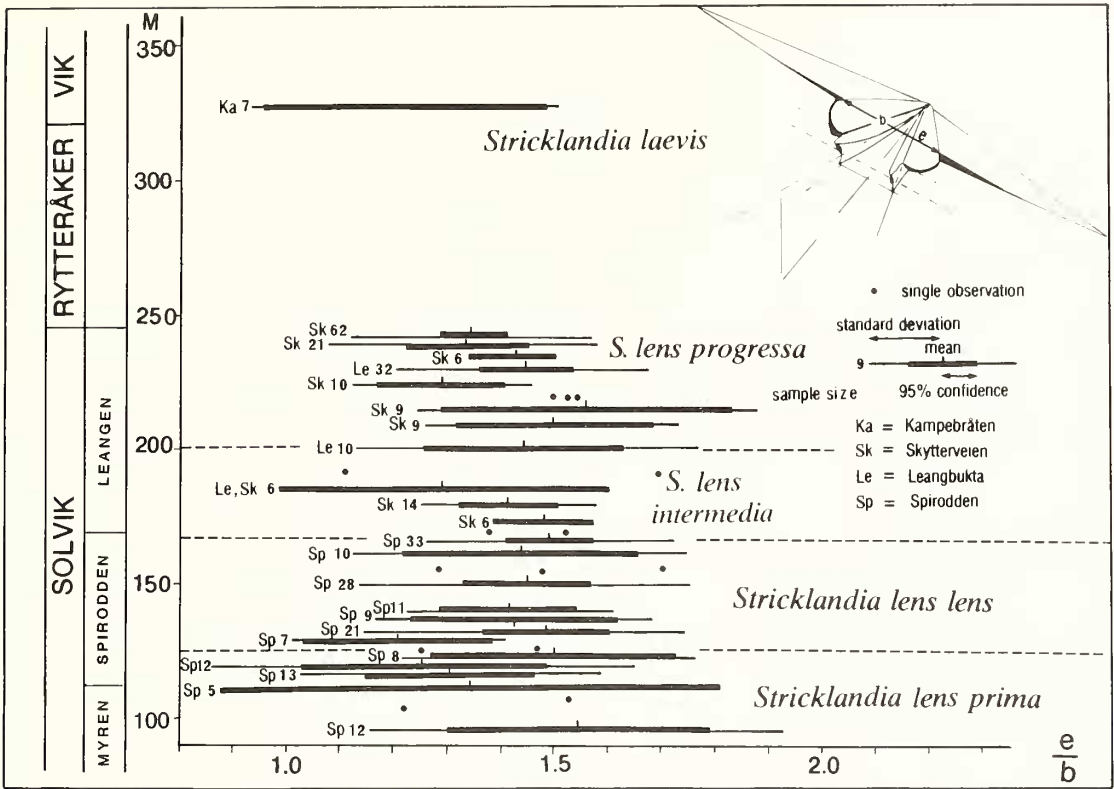
TEXT-FIG. 4. Mean, standard deviation, and 95% confidence intervals of form index d/b for all stricklandiid samples with sample size 5 or more in the Solvik Formation of the main Asker area, plotted against stratigraphic level. For comparison one sample from the Vik Formation in Sandvika is included.

TABLE 2. Correlation between the form indexes and valve size represented by maximum width of valve H and maximum length of interarea G expressed by the correlation coefficient and the students t-test.

Form indexes	a/b	f/b	d/b	e/b	c/b	$(a+c)/b$
Sample number	23	14	23	22	23	23
H, corr. coef.	0.1028	0.0666	0.0140	0.2100	0.5749	0.1749
T-test	-0.4957	-0.2497	-0.0673	-1.0075	3.3698	0.8520
Sample number	41	26	41	40	41	41
G, corr. coef.	0.2764	0.1025	0.3483	0.1073	0.0592	0.2541
T-test	-1.8417	-0.5258	-2.3798	-0.6828	-0.3797	-1.6827

not equalled in the main Asker area, but falls in a gap between the indexes for material from the uppermost Spirodden Member and lowermost part of the overlying Leangen Member. The Spirodden Member is considerably thicker in the Sandvika area than in the main Asker area and the probability of a diastem caused by non-deposition or erosion of the upper part of the member in the main Asker area is thus corroborated by the observations on *Stricklandia*.

The next samples from the Sandvika area are found at the top of the Solvik Formation. The indexes equal the indexes found in the top 20 m of the Solvik Formation in the main Asker area. Two samples



TEXT-FIG. 5. Mean, standard deviation, and 95% confidence intervals of form index e/b for all stricklandiid samples with sample size 5 or more in the Solvik Formation of the main Asker area, plotted against stratigraphic level. For comparison one sample from the Vik Formation in Sandvika is included.

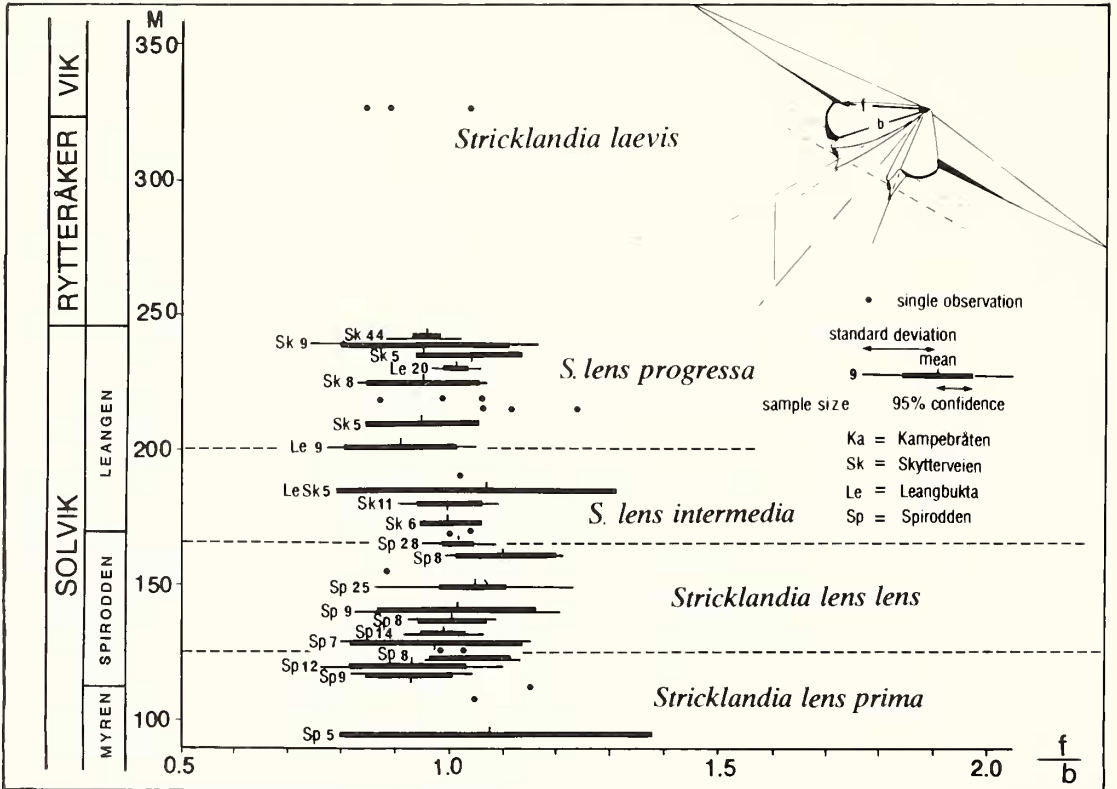
obtained from different localities exposing the basal Vik Formation in the Sandvika area have virtually identical form indexes.

Estonia

The Estonian material consisted of five subspecies determined semiquantitatively by Rubel (1977). The form indexes for these five groups show a strong, steadily decreasing and directed trend for a/b (text-fig. 11). The index c/b also decreases but shows a small reversal for the youngest taxa. Inspection of the raw data revealed that one specimen out of the five had indexes lying far from the rest. The result for c/b if this is omitted gives a steadily decreasing line (index = 0.18). The index d/b also decreases but shows reversals. Measurements for d could be obtained from only three specimens for each of the three youngest taxa, so the result is not very reliable. All the other measurements varied around a constant. The results from Estonia are thus consistent with the results obtained from the Norwegian material.

Comparison with the Llandovery type material

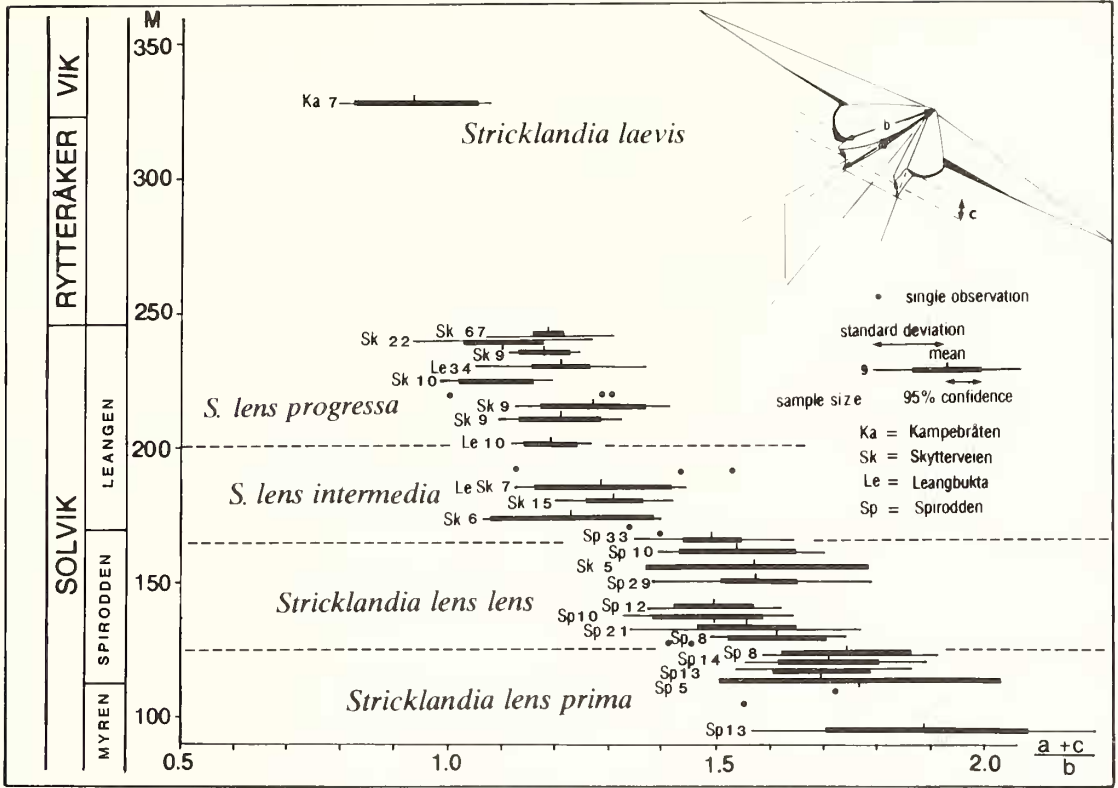
The measured type material consists of a very small sample with much phenotypic variation. It may be treated statistically, however, like the Estonian and Norwegian material. The two form indexes showing the strongest trends in the Norwegian, Estonian, and Llandovery material are a/b and c/b (text-fig. 11). They correspond to two of the trends described by Williams (1951) from the Llandovery



TEXT-FIG. 6. Mean, standard deviation, and 95% confidence intervals of form index f/b for all stricklandiid samples with sample size 5 or more in the Solvik Formation of the main Asker area, plotted against stratigraphic level. For comparison one sample from the Vik Formation in Sandvika is included.

material. The decrease in a/b (or the length of the outer plates relative to the length of the inner plates) corresponds directly to the reduction of the outer plates used by Williams (1951). The decrease in c/b (or the vertical distance from the anterior point of the inner plates to the valve floor relative to the length of the inner plates) is related to the decrease in angle between the inner plates and the base of the brachial processes plus outer plates described by Williams (1951) and further stressed by Rubel (1977). The third decreasing trend found in all material (text-fig. 11), index d/b , is directly related to the index a/b since d is the distance between the anterior point of the diverging and steadily decreasing outer plates. The form index d/b shows a stronger decreasing trend in the Welsh material than both the Norwegian and Estonian material, and the index for the Estonian material is consistently higher, so the angle between the plates must be environmentally determined. The gradual decrease found in f/b in the Llandovery material is not very large, and is not observed in the other material.

The size of the cardinalia in the subspecies studied by Williams (1951) shows a steady increase. This is explained by the massive development of the inner plates and their reorientation. The size is represented by the width of the cardinalia over the length of the interarea, and over the maximum width of the valve, giving the two indexes e/h and e/g . The form index e/g gives no directed trend for both areas. The form index e/h gives no directed trend for the Norwegian material. The Llandovery material (which only comprised six measurements for this index) had about equal indexes for the two oldest subspecies. The two youngest subspecies, however, showed a strong increase. It is questionable that any conclusions may be drawn from these few observations and it is supposed



TEXT-FIG. 7. Mean, standard deviation, and 95% confidence intervals of form index $(a + c)/b$ for all stricklandiid samples with sample size 5 or more in the Solvik Formation of the main Asker area, plotted against stratigraphic level. For comparison one sample from the Vik Formation in Sandvika is included.

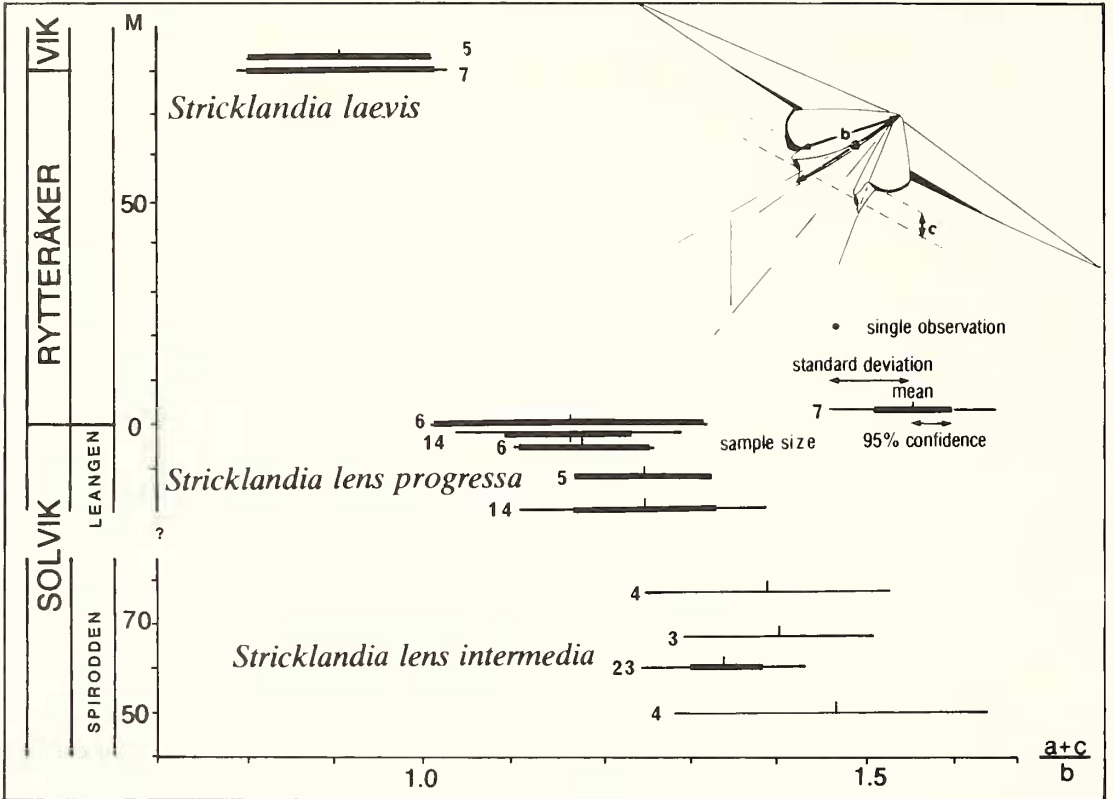
that Williams (1951) based his observations of increasing size on a much larger sample observed in the field.

A final but important feature which is not treated in this study is the impression of the muscle fields. They become larger and deeper with time, according to Williams (1951). Rubel (1977) considered this, and showed that the outline and pattern of the muscle scars also changed with time. Consistent changes have been observed non-quantitatively during this study.

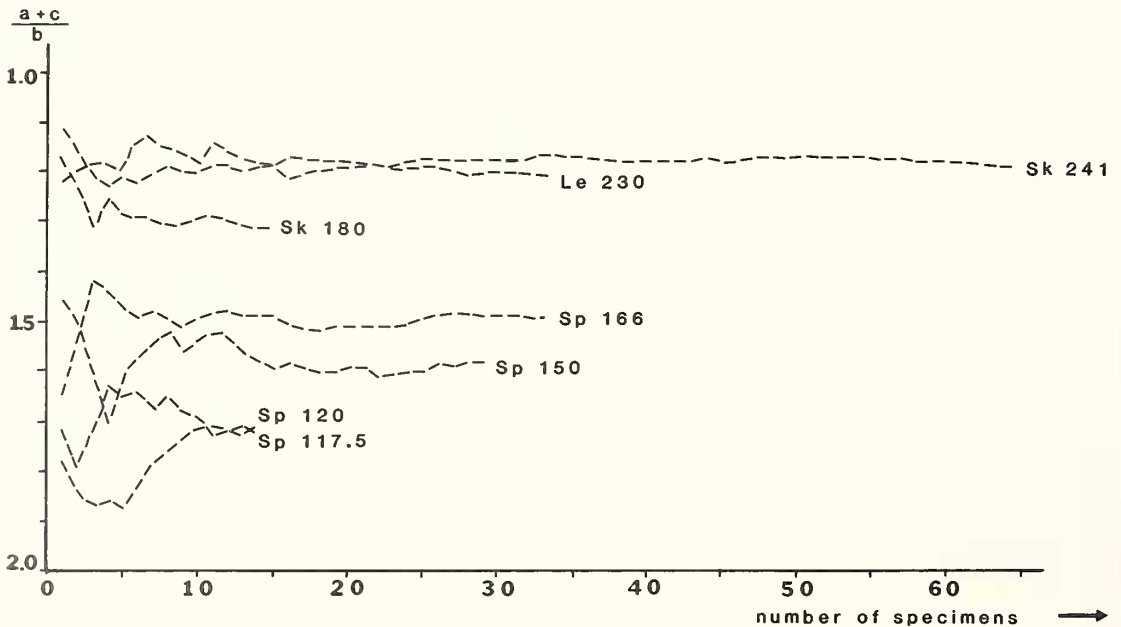
TAXONOMIC DETERMINATION OF SUBSPECIES

The stricklandiid subspecies were originally described by Williams (1951) and redescribed by Rubel (1977). The Norwegian material is assigned to subspecies accordingly. The indexes used in this study for the subspecies samples from the three geographic regions may be compared with one another to test their validity for taxonomic use.

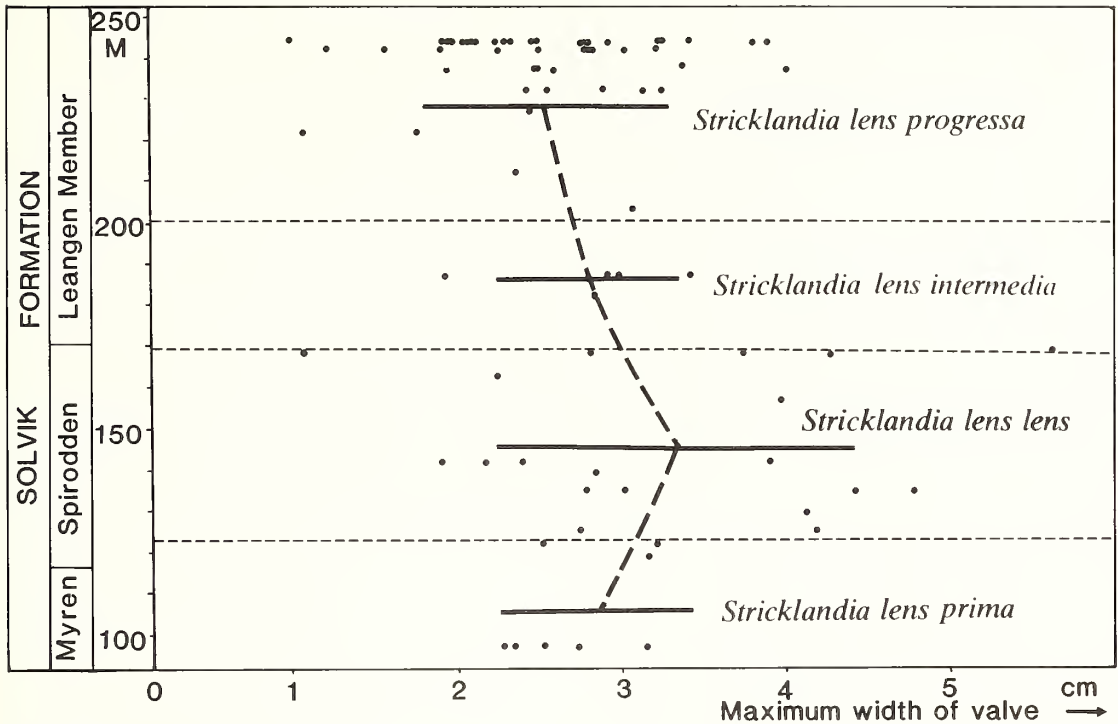
The Norwegian material often lacks features used in the definitions of subspecies such as the shape of the interarea, impression of the muscle fields, and presence or absence of fold and sinus. The size of cardinalia (used by Williams (1951)) is shown to be invalid for taxonomical use in *Stricklandia* in this study. The subspecies, as redefined by Rubel (1977), are still possible to distinguish in the Norwegian material, except for the two oldest. The definitions of these are difficult to apply to this material. Williams (1951) explicitly stated that the outer plates extend beyond the line of fusion with the brachial process in *S. lens prima* while they were only moderately long in the youngest subspecies. It



TEXT-FIG. 8. Mean, standard deviation, and 95% confidence intervals of form index $(a+c)/b$ for all stricklandiid samples with sample size 5 or more in the Solvik and Vik formations in Sandvika. 95% confidence intervals are not shown for smaller samples.



TEXT-FIG. 9. Dependence of sample size on the form index $(a+c)/b$ shown for the largest samples at different levels up through the Solvik Formation of the main Asker area.

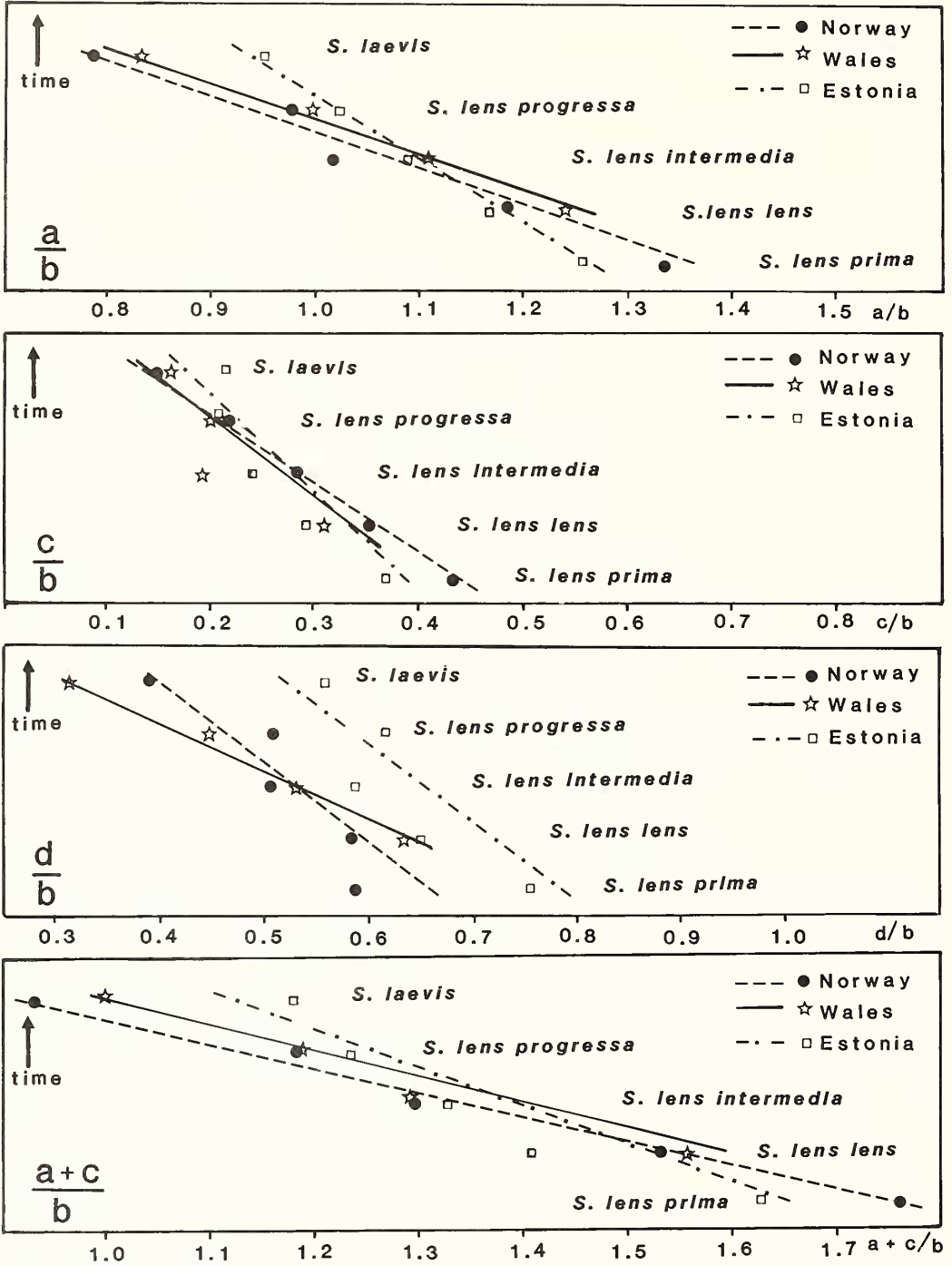


TEXT-FIG. 10. Single measurements and mean with standard deviation of maximum width of valve of subspecies plotted against stratigraphic level.

is, therefore, here proposed to add to the diagnosis that *S. l. prima* displays outer plates extending anteriorly beyond their fusion with the brachial process.

S. lens first occurs 11 m above the base of the Solvik Formation in the central Asker district (i.e. very near the base of the Silurian). No samples less than 95 m above the base were sufficiently large or well enough preserved to allow measurement for identification to subspecies. The samples from 95 m to 168 m above the base of the Solvik Formation show completely gradual changes in internal features. The lowest sample at 95 m above the formational base is the only one showing good external features. The specimens all have a very distinct fold and sinus. On this basis they belong to *S. l. prima*. All specimens from 95.0 m to 122.5 m have outer plates which extend far beyond their fusion with the brachial processes, while a few specimens above show shorter outer plates. There are very slight differences in samples from this level to 132.5 m above the formational base. The level at 122.5 m is chosen, however, to represent the uppermost limit of the subspecies *S. l. prima* as redefined here. *S. l. lens* occurs up to 168 m above the base of the Solvik Formation.

There is a pronounced difference in morphology between the specimens found up to 168 m above the formational base in the Spirodden Member and those found stratigraphically above in the Leangen Member. The reason for this is probably a diastem in the main Asker area. The specimens in the basal Leangen Member belong without a doubt to *S. l. intermedia*. The stratigraphic section of the Sandvika area is probably more complete and stricklandiids here are of an intermediate type. The available material is judged to belong to *S. l. intermedia*. A part of the range of this species is therefore missing in the main Asker area.



TEXT-FIG. 11. Plots of form index a/b , c/b , d/b , and $(a+c)/b$ for succeeding stricklandiid subspecies from main Asker area in Norway, Wales, and Estonia. The distances between the stricklandiid subspecies are kept equal without regard to actual time.

The transition to the next overlying subspecies is again very gradual and difficult to delimit. At 230 m above the formational base the populations belong to *S. l. progressa*, while the populations under 192 m above the formational base clearly belong to *S. l. intermedia*. The transition is somewhat arbitrary but there seems to be a majority of specimens with laterally wide splaying plates characteristic of the youngest subspecies from 202.5 m above the formational base. Specimens with degenerate outer plates are also observed, although very seldom from this level on.

The subspecies *S. laevis* is not found in the main Asker area but the specimens found at the base of the Vik Formation in the Sandvika area of the Asker district belong without any doubt to this species. The different Norwegian subspecies are shown in Plate 21.

The form indexes may be used to support the validity of stricklandiid subspecies in Norway as compared with Llandovery and Estonia. Text-fig. 11 plots the average form indexes of the different subspecies from the main Asker area in Norway, Llandovery, and Estonia for a/b , c/b , and d/b and for the combination $(a+c)/b$. All plots of form indexes lie within the standard deviation of the Norwegian material, and most plot very close together. The Estonian material has lower values for the indexes a/b and c/b for *S. leus prima* than seen in Norway. This may be the result of a shorter time interval represented by this subspecies (i.e. only the top range of *S. leus prima*). This is not possible to prove, however, with the available data. The very high value found for *S. laevis* in Estonia is influenced by one deviating specimen in a small sample, as discussed above.

Considering the small sample sizes in the Llandovery material and the exceptional cases explained above the indexes support the designation to subspecies made in Norway.

The best fit for all subspecies is seen for the index $(a+c)/b$. This form index therefore may be used to determine and distinguish subspecies more accurately, where the size of the sample is adequate.

SIMULTANEOUS OCCURRENCE IN WALES AND NORWAY

The two oldest types for *Stricklandia* in Wales come from the southern part of the Llandovery area where no determinative graptolites are known. Cocks *et al.* (1984) suggest a stratigraphic range for the lineage *S. leus/S. laevis* from the base of the *acinaces* graptolite biozone to mid-*griestouiensis* graptolite biozone, where *Costistricklandia lirata* takes over the succession. *Stricklandia* in Norway ranges from earliest Silurian time (late *persculptus* to early *acuminatus* graptolite biozone) to somewhere between the *turriculatus* and mid-*griestoniensis* graptolite biozones. Thus the upper limits of the lineage are coeval in Norway and Wales, while the first occurrence in Norway probably predates the oldest known representatives in Wales.

In the Llandovery area only the *S. leus progressa* to *S. laevis* and *S. laevis* to *C. lirata* transitions are well defined. None of the lower subspecies are found directly succeeding one another and only the biostratigraphic position of Williams's type specimens are implied (Cocks *et al.* 1984). In Norway the lowest four subspecies are found succeeding each other, while the upper transitions are not recognized.

The types of *S. leus prima* and *S. l. leus* are both placed in the *cyplus* graptolite biozone in the Llandovery area by Cocks *et al.* (1984). The same transition, based on a redefined *S. l. prima*, is set in Norway at 122.5 m above the base of the Solvik Formation. This may also occur in the *cyplus* zone, since the nearest datable stratum 170 m above the base is certainly younger than the uppermost *atavus* biozone, and probably as young as the *cyplus* biozone.

The transition between *S. l. leus* and *S. l. intermedia* is proposed in Norway at a horizon 168 m above the base of the Solvik Formation. Again this is probably within the *cyplus* graptolite biozone in Norway. The type of *S. l. intermedia* is found in the *convolutus* biozone, but Williams (1951) indicated that it ranges down to the top of the Rhuddanian or the *cyplus* biozone.

S. l. progressa is found in the Rhydings and Wormwood formations within the *sedgwickii* to lowermost *turriculatus* biozones (Cocks *et al.* 1984). The transition between this subspecies and the underlying *S. l. intermedia* must therefore occur within the *convolutus* biozone. The transition in Norway cannot be younger than the *gregarius* graptolite biozone. The very gradual transition could, however, justify a boundary set considerably higher up in the section perhaps into the *convolutus* biozone.

S. laevis found in Norway occurs at a level which is correlated to the *turriculatus* biozone and is well within the range of this species in Wales.

The correlation between Norway and Wales is hard to corroborate because of poor graptolite records in both areas. There is, however, no definite proof of a disparity in age for any of the taxa and the coincidental occurrence of the youngest taxa would deny the existence of a geographical cline.

SUMMARY AND CONCLUSIONS

1. The section in the main Asker area displays the four subspecies *S. lens prima*, *S. l. lens*, *S. l. intermedia*, and *S. l. progressa* in a continuous succession. The Sandvika area provides the lower range of *S. l. intermedia* missing in the main Asker area.

2. Plots of form indexes a/b and c/b grouped in subspecies after the definition of Rubel (1977) correlate well for Norway, Estonia, and Wales. Form index $(a+c)/b$ serves even better and may therefore be used as a biometric tool for determination of subspecies.

3. The total range of the stricklandiid lineage is roughly coeval in Wales and Norway. The subdivisions of the lineage *S. lens/S. laevis* may be temporally equivalent as well. No evidence for a geographic cline is observed.

4. Phenotypic variation within the populations are so large that phenotypes on the periphery of succeeding subspecies occur together. Preferred sample size should ideally be fifteen to twenty specimens with a minimum of ten specimens to ensure a reliable index mean.

5. The same decreasing trends in form indexes a/b , c/b , and d/b are found in two Norwegian sections, in Estonia, and in the Llandovery area of Wales. Form indexes a/b and c/b fall within the same range for the four sections, while d/b have different but always decreasing ranges. The combination index $(a+c)/b$ gives the clearest and strongest trend, with high correlation in the four investigated areas.

6. The only form index depending on valve size is c/b which shows a positive correlation. Valve size shows no trend up through the section and therefore cannot cause the observed decreasing trend in c/b which therefore is regarded to be evolutionary.

7. The trends expressed by form indexes a/b and c/b correspond to trends used by Williams (1951) and Rubel (1977) to distinguish stricklandiid subspecies. These are: 1, the outer plates are reduced relative to the inner plates; 2, the angle between inner plates and the bases of the brachial processes plus outer plates decreases.

8. The trend in increasing size of the interarea described by Williams (1951) and used to designate subspecies is not found in the Norwegian material and is regarded as environmentally controlled and invalid for discrimination of subspecies.

Most of the criteria of Gould and Eldredge (1977) for adequate tests on evolutionary models are met in this study. Two of the same decreasing trends are tested and found to occur within the same

EXPLANATION OF PLATE 21

Figs. 1 and 2. *Stricklandia lens prima* (Williams). Latex casts of brachial valve moulds, Solvik Formation, Spirodden, Asker. 1, P.M.O.108291, 117.5 m above the formational base, $\times 6$; 2, P.M.O.105246, 95 m above the formational base, $\times 8$.

Figs. 3 and 4. *S. l. lens* (Sowerby). Latex casts of brachial valve moulds, Solvik Formation. 3, P.M.O.108292, 130 m above the formational base, Spirodden, Asker, $\times 6$; 4, P.M.O.105852, 155 m above the formational base, Skytterveien, Asker, $\times 6$.

Fig. 5. *S. l. intermedia* (Williams). Latex cast of brachial valve mould. P.M.O.108293, 180 m above the base of the Solvik Formation, Skytterveien, Asker, $\times 6$.

Figs. 6 and 8. *S. l. progressa* (Williams). Latex casts of brachial valve moulds. 230 m above the base of the Solvik Formation, Leangbukta, Asker. 6, P.M.O.105252, $\times 6$; 8, P.M.O.108320, $\times 6$.

Fig. 7. *S. laevis* (Sowerby). Latex cast of brachial valve mould. P.M.O. 105254, 0.4 m above the base of the Vik Formation, Kampebråten, Sandvika, $\times 8$.



1



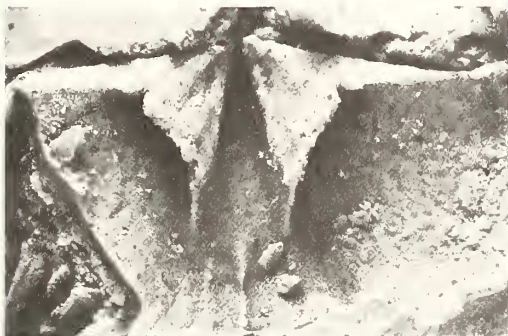
2



3



4



5



6



7



8

range in three widely separated areas under different sedimentary conditions. Williams's definition (1951) of stricklandiid subspecies withstands rigorous testing in all but one respect: size increase of the cardinalia through time. The Norwegian stratigraphic sequences are long and provide reasonably large samples, although not large or closely spaced enough to reveal with certainty the fine details of micro-evolution.

The evolution of *Stricklandia*/*Costistricklandia* is generally considered to be phyletic (Boucot 1975; Johnson 1979). Due to unavoidably coarse sample intervals this study cannot test that view with statistical certainty for any of the studied sections. The exhibited trends are, however, found in four different sections. They are seemingly gradual, linear, and simultaneous over a wide geographic area, and strongly suggestive of orthoselection and possibly phyletic gradualism. Whatever the fine-scale pattern of evolution is, the *Stricklandia*/*Costistricklandia* lineage has been, and still is, of prime importance for the biocorrelation of shelly faunas in Llandovery sections all over the world.

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